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BLOOD SAMPLING REDUCES ANNUAL SURVIVAL IN CLIFF SWALLOWS (*PETROCHELIDON PYRRHONOTA*) -- La Toma de Muestras de Sangre Reduce la Supervivencia Anual en *Petrochelidon pyrrhonota*

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BLOOD SAMPLING REDUCES ANNUAL SURVIVAL IN CLIFF SWALLOWS (*PETROCHELIDON PYRRHONOTA*)

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Abstract.—Researchers commonly collect blood samples from wild birds, and most workers assume that blood sampling has no adverse effect on the birds' survival. Few studies, however, have done controlled comparisons among bled and non-bled individuals and estimated survival using modern statistical methodology. We used a data set on Cliff Swallows (*Petrochelidon pyrrhonota*) that included 2,945 bled and 7,822 non-bled birds captured at the same times and sites in southwestern Nebraska from 1986 to 2006 to estimate annual survival and recapture probabilities of each group. Blood was collected with brachial venipuncture in amounts varying from 0.3% to 1.2% of the birds' body mass. Apparent survival of bled birds was lower than that of non-bled birds: bled birds experienced a 21–33% reduction in average survivorship, depending on amount of blood taken and whether the individuals were resident at a fumigated (parasite-free) or non-fumigated colony at the time of sampling. The percent reduction in annual survival was higher for individuals at non-fumigated colonies. All effects of blood sampling applied only in the year after sampling, and there were no effects in later years. Our results suggest that brachial blood sampling is not a benign technique. Researchers following the 1%-of-body-mass guideline may be collecting too much blood from wild birds, especially when research requires repeated samples over short periods *Received 3 March 2009, accepted 3 May 2009.*

Key words: blood sampling, Cliff Swallow, *Petrochelidon pyrrhonota*, research techniques, survival.

La Toma de Muestras de Sangre Reduce la Supervivencia Anual en *Petrochelidon pyrrhonota*

Resumen.—Comúnmente los investigadores recolectan muestras de sangre de aves silvestres, y en la mayoría de los casos se supone que el muestreo de sangre no tiene efectos adversos sobre la supervivencia de las aves. Sin embargo, pocos estudios han realizado comparaciones controladas entre individuos a los que se les tomó una muestra de sangre e individuos no muestreados, estimando su supervivencia utilizando técnicas estadísticas modernas. Utilizamos una base de datos de capturas de *Petrochelidon pyrrhonota* que incluía 2,945 individuos a los que se les tomó una muestra de sangre y 7,822 individuos no muestreados capturados al mismo tiempo y en los mismo sitios en el sudoeste de Nebraska desde 1986 a 2006, para estimar la supervivencia anual y las probabilidades de recaptura de cada grupo. Las muestras de sangre fueron recolectadas por medio de una punción en la vena braquial en cantidades que variaron entre un 0.3% a 1.2% de la masa corporal del individuo. La supervivencia aparente de las aves muestreadas fue menor que la de las aves no muestreadas. Las aves muestreadas presentaron una reducción del 21–33% en su supervivencia media, dependiendo de la cantidad de sangre que fue recolectada y si el individuo era residente de una colonia fumigada (libre de parásitos) o no fumigada en el momento del muestreo. El porcentaje de reducción en la supervivencia anual fue mayor para los individuos de colonias no fumigadas. Todos los efectos de la toma de muestras de sangre sólo se aplicaron al año siguiente del muestreo, y no hubo efectos en años posteriores. Nuestros resultados sugieren que la colección de sangre de la vena braquial no es una técnica benigna. Los investigadores que han seguido la recomendación de extraer hasta un 1% de la masa corporal podrían estar recolectando demasiada sangre de aves silvestres, especialmente si la investigación requiere muestreos repetidos en intervalos de tiempo cortos.

Researchers commonly collect blood samples from wild birds in the field. Many studies on hormones, parentage, immunocompetence, parasite and disease exposure, and population genetics often require the collection of blood for harvesting of plasma, detection of pathogens or antibodies, isolation of DNA, molecular sexing, or other purposes (Sheldon et al. 2008). The prevailing assumption among most researchers is that blood sampling has little or no effect on birds, if done properly. The basis for this belief appears to stem from several oft-cited papers on various species (Raveling 1970, Wingfield and Farner 1976, Bigler et al. 1977, Gowaty and Karlin 1984, Frederick 1986, Stangel 1986, Dufty 1988; reviewed in Sheldon et al. 2008). The statement in the

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Ornithological Council's *Guidelines to the Use of Wild Birds in Research* (Gaunt and Oring 1999) that blood collection does not affect avian survival is apparently based on these studies, even though this work (and other, similar studies) either measured survival in captive birds only, did not have adequate controls using non-bled birds handled the same way at the same time, asserted that bleeding had no effect without presenting data, or measured only resighting–recapture percentages without statistically valid estimates of actual survival. Furthermore, the *Guidelines* suggested that the volume of collected blood can be up to 1–2% of a bird's body mass (Gaunt and Oring 1999). However, this recommendation is apparently based only on laboratory studies of mammals (McGuill and Rowan 1989).

We have found no studies that measured the effect of either blood sampling *per se* or sampling of various amounts of blood on annual survival probability, using individuals handled the same way at the same time, but not bled, and subjected to modern statistical estimates of survival that control for potential differences in recapture rates or detectability among classes of individuals (*sensu* Lebreton et al. 1992). If blood sampling negatively affects survival, this presents ethical issues in general, conservation issues for endangered or threatened species in particular, and scientific issues when, for example, population-level demographic processes are inferred, at least in part, on the basis of bled birds.

Using a long-term mark–recapture data set on colonially nesting Cliff Swallows (*Petrochelidon pyrrhonota*), we investigated how blood sampling affected annual survival in this species. Between 1986 and 2001, blood samples were taken from Cliff Swallows for various projects investigating parentage (Brown and Brown 1988), immunocompetence (Møller et al. 2001), hormone levels (Brown et al. 2005a, b; Smith et al. 2005; Raouf et al. 2006), and exposure to viruses (C. Brown et al. unpubl. data). The survival of these birds, and that of individuals captured at the same colony sites at the same times but not bled, was monitored by extensive mark–recapture efforts in the study area each year through 2006 (e.g., Brown and Brown 2004; Brown et al. 2005a, b, 2008). Using mark–recapture modeling (Lebreton et al. 1992, White and Burnham 1999, Burnham and Anderson 2002), we compared annual survival of bled and non-bled birds by year and investigated how collection of different amounts of blood potentially affected long-term survival. To our knowledge, this is the first study to formally apply a modern mark–recapture statistical analysis of how blood sampling affects survival using paired comparisons of bled and non-bled birds initially captured at the same time.

Methods

Study site.—Cliff Swallows have been studied since 1982 near the Cedar Point Biological Station (41°13′N, 101°39′W) in Keith County, southwestern Nebraska, along the North Platte and South Platte rivers; the study area also includes portions of Deuel, Garden, and Lincoln counties. Cliff Swallows construct gourd-shaped mud nests, often in dense, synchronously breeding colonies. In our study area, they nest mostly on the sides of bridges, in box-shaped road culverts, or underneath overhangs on the sides of cliffs. The study area contains ~170 colony sites, about a third of which are not used in a given year. Colony size varies widely; in our study area, it ranges from 2 to 6,000 nests (mean = 393 ± 15 [SE]; n = 1,812 colonies), with some individuals nesting solitarily. The study site is described in detail by Brown and Brown (1996).

Beginning in 1984 and continuing throughout the study, we fumigated selected colonies each year to remove Swallow Bugs (Cimicidae: *Oeciacus vicarius*), the principal Cliff Swallow nest ectoparasite. Nests within colonies were sprayed with a dilute solution of an insecticide, Naled (trade name Dibrom), which was highly effective in killing Swallow Bugs (Brown and Brown 1986, 1996). Nests were fumigated frequently to remove any bugs brought into the colony by transient birds. Because both daily and annual survival in Cliff Swallows can be influenced by the extent of ectoparasitism at a colony (Brown and Brown 1996, 2004; Brown et al. 2005a), we tested for effects of fumigation in analyzing differences in survival between bled and non-bled birds.

Blood sampling.—In 1986 and 1987, adult Cliff Swallows were blood-sampled for a parentage study (Brown and Brown 1988) by capturing them inside their nests; other adults were captured at the same time with the same method but not blood-sampled. Nests for the parentage study—and, thus, the individuals chosen to be bled—were selected haphazardly without predefined selection criteria and with no knowledge of the nest owners' phenotypic characteristics. Bleeding was restricted to a set number of nests because of logistical and financial constraints on how many samples could be processed, and individuals from nests that we did not need for the parentage study served as the "non-bled" comparison. In four years, as part of a hormone study, we haphazardly selected a subset of individuals mist-netted at selected colony sites for blood sampling. We chose individuals for sampling in 1993, 1997, 2000, and 2001 solely on the basis of our ability to process them within 3 min of their first encountering the net, as required by the hormone-analysis protocol (Brown et al. 2005a, b; Smith et al. 2005; Raouf et al. 2006). We did not select individuals with particular phenotypic characteristics for the hormone studies, other than trying to balance the number of males and females sampled. In 1998 and 1999—for studies of immunocompetence (Møller et al. 2001) and seroprevalence to an arbovirus (C. Brown et al. unpubl. data), respectively—we haphazardly selected individuals to bleed without regard to how long they had been in the net. In Møller et al.'s (2001) study, all birds bled in 1998 were used to assess immunological response to challenge with phytohemagglutinin and sheep red blood cells, which required that they be injected with these substances. About 25% of these birds were recaptured either 24 h or seven days later for subsequent measurements.

In the present study, individuals not bled in each year were those captured in mist nets or in nests on the same days, at the same times of day, and at the same colony sites as the bled birds. For example, on each occasion at a given site when we collected blood, any non-bled bird captured on that day at that site would be added to the "non-bled" data set. Non-bled birds captured at other times (when no blood sampling occurred) were not included; this method ensured that the populations of bled and non-bled birds were similar with respect to capture date, colony size, nesting stage, nesting substrate (bridge vs. culvert), and other variables, although sample sizes tended to be larger for non-bled birds simply because we usually captured far more than we could bleed at any one time. Handling differed, however, between bled and non-bled birds, because those not bled were not held in the bleeding posture (i.e., no sham-bleeding was done). Non-bled birds captured at

TABLE 1. Numbers of bled birds and non-bled birds, and the workers (A–D) doing the blood sampling of Cliff Swallows each year of the study.

Year	Bled birds	Non-bled birds	Worker(s)
1986	182	387	A
1987	192	51	A
1993	61	78	B
1997	36	49	A
1998	190	787	C
1999	248	395	A
2000	1010	3299	B, D
2001	1026	2826	B, D

the same time as the bled birds in the immunocompetence study (Møller et al. 2001), including during the recapture occasions, were not subjected to injections (although otherwise treated the same). As with the birds that were bled, we did not systematically select individuals with certain phenotypic characteristics for the non-bled group in any of the years.

Four workers bled birds during the study. These were trained, relatively senior investigators with considerable experience bleeding and handling birds; none of the bleeding was done by inexperienced (e.g., seasonal or student) assistants. The numbers of birds bled and not bled and the workers who sampled blood (A–D) in each year of the study are listed in Table 1. Over all years, we had a total of 2,945 birds bled and 7,822 birds not bled. Only adult birds (those ≥1 year old) are considered here. The amount of blood taken and the sites sampled (fumigated or non-fumigated) differed among years, depending on the projects being done that required blood.

All blood was sampled from the brachial vein using a 26-gauge needle or lancet. There appeared to be no systematic differences in the wound produced or blood lost during collection when using either needles or lancets. Blood was collected in 70-μL capillary tubes. We classified bled birds into two groups: those for which a "small" amount of blood was taken (i.e., one to two capillary tubes, or approximately 70–140 μL; this was 0.3–0.6% of body mass, assuming an average mass of 23 g for Cliff Swallows at our study site), and those for which a "large" amount of blood was taken (three to four capillary tubes or approximately 210–280 μL; 0.9–1.2% of body mass). These amounts were approximations, because in many cases one or more tubes were not full or additional blood loss (e.g., hematomas) occurred after we filled the tubes. When we were unsuccessful in drawing blood even though we may have pricked the skin, we excluded the individual from analyses.

Mark–recapture.—Cliff Swallows were mist-netted at 27–40 colonies in the study area each year from 1986 through 2006. Although blood sampling occurred at only a subset of these sites, all recaptures from throughout the study area were used in estimating survival, because Cliff Swallows often move to different colony sites between years. Nest owners were captured in nests by plugging the nest entrances with cotton at night, then extracting the birds at dawn. Mist nets were erected across the entrances to culverts or along the sides of bridges; at some sites, we dropped nets from the top of the bridge, catching residents when they flushed from their nests. The netting method is described more fully elsewhere (Brown and Brown 1996, 2004; Brown 1998). The number of days on which we mist-netted birds at a colony site in a given year varied from 1 to 37, depending on the ease of netting there, the colony size, colony phenology, or other considerations. All birds captured were banded with a U.S. Geological Survey numbered aluminum leg band (upon first capture), sexed by the presence of a cloacal protuberance or brood patch, and weighed with a Pesola scale by placing the bird in a cloth bag. Beginning in 1996, morphological measurements were taken on a smaller subset (e.g., Brown and Brown 1998, 2002) without regard as to whether they were also blood-sampled.

Statistical estimation of survival.—A multistate capture–recapture history was constructed for each bled and non-bled bird, beginning with the year that each was bled or (for non-bled birds) the year in which it was paired with a blood-sampling occasion. Capture histories for years prior to bleeding or that served as a "non-bled" comparison were disregarded, and, thus, survival was estimated for both bled and non-bled birds only over the years after the bleeding event. Each bird was assigned one of the following six states in each year, beginning with the year it first entered the data set: (1) small amount of blood taken and bird captured at a fumigated colony; (2) large amount of blood taken and bird captured at a fumigated colony; (3) small amount of blood taken and bird captured at a non-fumigated colony; (4) large amount of blood taken and bird captured at a non-fumigated colony; (5) no blood taken and bird captured at a fumigated colony; and (6) no blood taken and bird captured at a non-fumigated colony. This enabled us to take into account transitions between states for the same bird in estimating survival; for example, we could thus account for cases in which a bird was bled and then captured in a later year but not bled. The total data set comprised 10,767 birds.

We fit models and estimated annual survival using the general methods of Lebreton et al. (1992) and Burnham and Anderson (2002). We used MARK (White and Burnham 1999) to assess the fit of different models to a given data set (and, thus, the support of different hypotheses) and to generate maximum-likelihood estimates of survival and recapture probabilities. Our previous analyses of survival in Cliff Swallows (e.g., Brown and Brown 1996, 2004; Brown et al. 2005a, b) had demonstrated that both annual survival and annual recapture probabilities tend to vary with year and to differ between birds in fumigated and non-fumigated colonies, so we had an *a-priori* basis for model-building. We tested specific hypotheses about the effect of blood sampling by modeling survival of bled and non-bled birds and those from fumigated and non-fumigated sites as different and then as the same, and in this way tested whether annual survival or recapture differed between categories of birds.

Model fit was assessed with Akaike's information criterion (Burnham and Anderson 2002), corrected for sample size (AIC_c) as provided by MARK. In theory, the model with the lowest AIC_c is the so-called best model. Because our data set did not meet the variance assumptions inherent in the binomial distribution used in mark–recapture analysis, we used quasi-likelihood (Burnham and Anderson 2002) to adjust model fit and variance of parameter estimates by calculating an overdispersion parameter, $\hat{c}$, using the combined chi-square value based on the multistate goodness-of-fit tests 2 and 3 in U-CARE (Pradel et al. 2005). A $\hat{c}$ value of 2.68 was used in MARK to substitute a $QAIC_c$ for the AIC_c, the $QAIC_c$ values being used for model selection and parameter estimation. This variance inflation adjustment allows use of data sets that depart from the assumptions of the binomial distribution (Wedderburn 1974, Burnham and Anderson 2002, Pradel et al. 2005). Because MARK may occasionally miscount the estimable parameters in a model, the number of parameters as given in MARK outputs was checked manually and adjusted (along with $QAIC_c$) where necessary. Apparent discrepancies among models in parameter counts were evidently caused by sparseness of data for some years or cohorts that prevented some parameters from being estimated.

To examine whether any effect of bleeding applied across all years or only to the year immediately after bleeding, we used age-structured models in which "first-year" survival equated to the year immediately following bleeding. Models with full age dependence and survival of bled and non-bled birds modeled separately tested whether survival was affected in all years after bleeding. Models with first-year survival considered separately for bled and non-bled birds, with survival in years beyond the first year considered the same for bled and non-bled birds, tested for an effect only in the year following blood sampling. Because annual survival does not vary with sex in our study population (Brown and Brown 1996), we did not separate the sexes for analysis. Beginning with relatively simple models, we added biologically relevant model structure in a systematic, balanced design, in which survival, recapture, and (to a lesser extent) transition probabilities were allowed to vary in different combinations of time-dependence, age-dependence, and effect of blood collection.

Results

Of the 24 total models fit to the data in exploratory analyses, 15 that either fit best or were relevant to hypothesis testing are shown in Table 2. The top model, with a $QAIC_c$ weight of ~0.97, showed that annual survival and recapture probabilities varied by year and differed between individuals captured at fumigated and non-fumigated colonies (Table 2), which is consistent with earlier analyses of this population. The top model also showed that survival differed with bleeding status, individuals from which a small amount was taken differing from those from which a large amount was taken and both differing from non-bled birds. An otherwise equivalent model without an effect of bleeding (survival of bled and non-bled birds modeled the same) ranked considerably lower (model 12; Table 2). A model that considered survival to be the same for birds from which a small amount of blood was taken and those not bled, but different for birds from which a large amount was taken, was the second-ranked model but still had relatively little support (model 2; Table 2). The effect of bleeding applied only in the first year after blood collection. A model with survival affected by blood sampling in all years after initial bleeding (model 6; Table 2) had far less support than one that considered subsequent-year survival to be the same among all "bled" and "non-bled" categories.

The top model (model 1; Table 2) had recapture probability varying with year and fumigation status, as in past analyses, but unaffected by whether birds were bled or not. Transition probabilities between the different blood and fumigation categories varied by transition type. Time- (year) and fumigation-dependent transition models would not converge, probably because they were overparameterized in relation to the data. Transition probabilities were small and averaged 0.0548 (± 0.0017) across the various transition combinations.

In 12 of 13 separate comparisons between bled and non-bled birds (differing by amounts taken and colony fumigation status by year), bled individuals had lower annual survival than non-bled ones, sometimes markedly so (Table 3). Survival and recapture estimates were taken exclusively from model 1 (Table 2), because no other models had enough support to merit model averaging. The average percent reduction in annual survival for bled birds, compared with non-bled individuals captured at the same times, was 27.3% and 33.0% for those from which a small amount of blood was taken at fumigated and non-fumigated colonies, respectively, and 21.7% and 28.9% for those from which a large amount was taken at fumigated and non-fumigated colonies, respectively (Table 3).

Discussion

Our analyses show clearly that Cliff Swallows that had blood samples collected from them survived less well than non-bled individuals captured at the same time and at the same colonies. Overall, blood sampling resulted in a 21–33% reduction in average annual survival probability, and the reduction in survival seemed broadly similar for all bled birds, irrespective of the amount of blood taken or whether birds were sampled at fumigated or non-fumigated colonies. The reduction in annual survival applied only to the year immediately after blood sampling, and there was no effect of blood sampling on survival in later years.

The commonly cited studies that reported no effect of blood sampling on survival in birds all used the percentage of bled birds that were resighted or recaptured to infer survival over periods ranging from a few days to a year (Franks 1967, Raveling 1970, Bigler et al. 1977, Frederick 1986, Colwell et al. 1988, Lanctot 1994, Brown 1995, Lubjuhn et al. 1998). In another study, the bled and non-bled birds were sampled in different years (Dufty 1988), and in another the conclusions applied only to birds kept in captivity (Stangel 1986). Other workers have also used recapture percentages to conclude that blood sampling has no adverse effects (Hoysak and Weatherhead 1991, Ardern et al. 1994, Perkins et al. 2004, Sheldon et al. 2008). Recapture percentage (especially for a single period) can be misleading, however, because it does not take into account temporary emigration from a study area or differences in detectability among groups of birds. For example, if birds selected for blood sampling are ones that are inherently more likely to be captured in a net ("trap-happy" birds), their recapture rate may be higher than that for more trap-shy, non-bled birds, and the inflated recapture rate could mask a lower true survival for the bled group and lead to erroneous conclusions about the effect of blood sampling. As an illustration, assume we release 200 bled and 200 non-bled birds. The bled birds have a true survival probability of 0.50, whereas the non-bled birds have a true survival probability of 0.75. This means that 100 bled birds and 150 non-bled birds are alive at the next capture occasion. But if the recapture probability for the bled birds was for example, 0.50, and that for the non-bled birds 0.33, perhaps because of differences in detectability, we would recapture 50 birds of each group. If we were basing our inference only on the observed percentage of the total birds marked, we would then erroneously infer survival of both groups to be 50 out of 200.

TABLE 2. Multistate models to estimate annual survival (ϕ), recapture (p), and state-transition (ψ) probabilities in Cliff Swallows in relation to whether blood was sampled, the amount of blood collected (small amount: 70–140 µL; large amount: 210–280 µL), and whether a colony was fumigated. Model notation is defined in the model description, and use of Akaike's information criterion (AIC) is described in the text.

Model	$QAIC_c$	$\Delta QAIC_c$	$QAIC_c$ weight	Number of estimable parameters	Description
(1) $\phi_{(t\text{-}f\text{-}b,1st\ year*amt)}, p_{(t\text{-}f)}, \psi_{(c\text{-}s)}$	14,791.226	0.00	0.96680	110	Survival varied by year (t) and was different for fumigated vs. non-fumigated colonies (f). Blood sampling (b) varied by year and amount (year*amt), with bled and non-bled birds modeled separately in the first year after bleeding but in the same way in all other years. Recapture varied by year and was different for fumigated vs. non-fumigated colonies. Transitions between bled and non-bled states were constant across years (c) and the same for fumigated and non-fumigated colonies, differing only by transition type (s).
(2) $\phi_{(t\text{-}f\text{-}b,1st\ year*amt,\ sm=n)}, p_{(t\text{-}f)}, \psi_{(c\text{-}s)}$	14,797.999	6.77	0.03270	104	Same as model 1 except that survival of birds with small amounts of blood taken (sm) was modeled in the same way as survival of those not bled (n).
(3) $\phi_{(t\text{-}f\text{-}b,1st\ year)}, p_{(t\text{-}f)}, \psi_{(c\text{-}s)}$	14,806.362	15.14	0.00050	100	Same as model 1 except that no distinction was made among birds from which large or small amounts of blood were taken.
(4) $\phi_{(t\text{-}f\text{-}b,1st\ year*amt)}, p_{(t\text{-}f\text{-}1st\ year)}, \psi_{(c\text{-}s)}$	14,817.286	26.06	0.00000	124	Same as model 1 except that recapture was modeled for the first year separately from all other years.
(5) $\phi_{(t\text{-}f\text{-}b,1st\ year)}, p_{(t\text{-}f\text{-}b,1st\ year)}, \psi_{(c\text{-}s)}$	14,819.316	28.09	0.00000	125	Same as model 3 except that recapture probability varied with blood sampling (no distinction between birds from which small or large amounts were taken, recapture for first year after bleeding modeled separately from all other years) and was the same within each fumigation category.
(6) $\phi_{(t\text{-}f\text{-}b,1st\ year*amt,\ 2nd\ year)}, p_{(t\text{-}f)}, \psi_{(c\text{-}s)}$	14,821.106	29.88	0.00000	185	Same as model 1 except that survival past the first year (2nd year) was modeled separately for each "bled" or "non-bled" category and for each fumigation status.
(7) $\phi_{(t\text{-}f\text{-}b,1st\ year*amt)}, p_{(t\text{-}f\text{-}b,1st\ year*amt)}, \psi_{(c\text{-}s)}$	14,821.855	30.63	0.00000	130	Same as model 4 except that recapture the first year was modeled differently for birds from which small amounts of blood were taken, those from which large amounts were taken, and those not bled.
(8) $\phi_{(t\text{-}f\text{-}b,1st\ year*amt)}, p_{(t)}, \psi_{(c\text{-}s)}$	14,862.196	70.97	0.00000	90	Same as model 1 except that recapture probability did not vary with fumigation status.
(9) $\phi_{(t\text{-}f\text{-}b,1st\ year*amt)}, p_{(t\text{-}1st\ year)}, \psi_{(c\text{-}s)}$	14,870.563	79.34	0.00000	97	Same as model 8 except that recapture was modeled for the first year separately from all other years.
(10) $\phi_{(t\text{-}f\text{-}b*amt)}, p_{(t)}, \psi_{(c\text{-}s)}$	14,893.099	101.87	0.00000	80	Fully time-dependent survival for each "bled" or "non-bled" category and for each fumigation status, but first year was not modeled differently from later years. Time-dependent recapture did not vary with bled or non-bled status or with fumigation status. Transitions as in model 1.
(11) $\phi_{(t\text{-}f\text{-}b,1st\ year*amt)}, p_{(t\text{-}f\text{-}b,1st\ year*amt,\ 2nd\ year)}, \psi_{(c\text{-}s)}$	14,957.158	165.93	0.00000	209	Same as model 1 except that recapture was modeled separately for first year vs. all others for each "bled" or "non-bled" category and for each fumigation status.
(12) $\phi_{(t\text{-}f)}, p_{(t\text{-}f)}, \psi_{(c\text{-}s)}$	14,977.997	186.77	0.00000	98	Same as model 1 except that no distinction was made between bled and non-bled birds.
(13) $\phi_{(t)}, p_{(t)}, \psi_{(c\text{-}s)}$	15,264.399	473.17	0.00000	46	Same as model 10 except that survival of bled and non-bled birds was modeled in the same way and did not vary with fumigation status.
(14) $\phi_{(f\text{-}b)}, p_{(t)}, \psi_{(c)}$	17,832.997	3,041.7	0.00000	27	Survival was constant with time but modeled separately for each "bled" and "non-bled" category and for each fumigation category. Recapture was time-dependent but did not otherwise vary. Transition was constant across all years, categories, and transition types.
(15) $\phi_{(t)}, p_{(t)}, \psi_{(c)}$	18,099.902	3,301.9	0.00000	40	Survival and recapture as in model 13, transition as in model 14.

Table 3. Annual survival (ϕ) and recapture (p) probabilities in the first year following blood sampling for Cliff Swallows from which we took a large (210–280 µL) or small (70–140 µL) amount of blood and for those not bled but captured at the same time each year at fumigated or non-fumigated colonies. Survival and recapture estimates were obtained from model 1 in Table 2.

	$\phi \pm$ SE	$p \pm$ SE
1986		
Large amount, fumigated	0.5213 ± 0.0898	0.3734 ± 0.0793
Not bled, fumigated	0.6364 ± 0.1257	0.3734 ± 0.0793
Large amount, non-fumigated	0.0973 ± 0.1561	0.2157 ± 0.0839
Not bled, non-fumigated	0.3049 ± 0.1325	0.2157 ± 0.0839
1987		
Large amount, fumigated	0.4853 ± 0.0806	0.5138 ± 0.0725
Not bled, fumigated	0.9099 ± 0.0003	0.5138 ± 0.0725
1993		
Small amount, fumigated	0.6470 ± 0.0309	0.5196 ± 0.2403
Not bled, fumigated	0.8380 ± 0.0314	0.5196 ± 0.2403
Small amount, non-fumigated	0.0378 ± 0.0619	0.4824 ± 0.2062
Not bled, non-fumigated	0.1376 ± 0.1132	0.4824 ± 0.2062
1997		
Large amount, non-fumigated	0.3417 ± 0.1905	0.2388 ± 0.1407
Not bled, non-fumigated	0.5036 ± 0.2574	0.2388 ± 0.1407
1998		
Small amount, fumigated	0.5669 ± 0.0539	0.7213 ± 0.0589
Not bled, fumigated	0.8308 ± 0.0229	0.7213 ± 0.0589
Small amount, non-fumigated	0.9156 ± 0.1878	0.1665 ± 0.0317
Not bled, non-fumigated	0.9510 ± 0.0005	0.1665 ± 0.0317
1999		
Small amount, non-fumigated	0.4862 ± 0.0850	0.3906 ± 0.0585
Not bled, non-fumigated	0.6309 ± 0.0820	0.3906 ± 0.0585
2000		
Large amount, fumigated	0.6705 ± 0.1071	0.5875 ± 0.0351
Not bled, fumigated	0.8329 ± 0.0440	0.5875 ± 0.0351
Large amount, non-fumigated	0.5363 ± 0.0562	0.2909 ± 0.0284
Not bled, non-fumigated	0.5155 ± 0.0434	0.2909 ± 0.0284
2001		
Large amount, fumigated	0.6228 ± 0.0352	0.5069 ± 0.0307
Not bled, fumigated	0.6392 ± 0.0649	0.5069 ± 0.0307
Large amount, non-fumigated	0.2873 ± 0.0288	0.3905 ± 0.0290
Not bled, non-fumigated	0.3559 ± 0.0431	0.3905 ± 0.0290

Survival is best estimated from models that explicitly account for differences in the likelihood of recapture or resighting (Lebreton et al. 1992). In our case, we were able to follow all cohorts for at least five years after blood sampling, which increased the likelihood that birds not detected in one year (e.g., the year after bleeding) but alive could be encountered in a later year. This allowed robust estimates of survival, and it may explain why our results are in contrast to previous work that made inferences based only on resightings during a single period (usually within a year of blood sampling).

Blood sampling affected survival in Cliff Swallows, but apparently only over the short term. Annual survival in the year after sampling (as measured to the next breeding season) was reduced, an expected result even if most of the sampling-induced mortality occurred in the first few days after blood collection. There was no evidence of any long-term effect of blood sampling in subsequent years; some bled birds lived ≥9 years after sampling and were ≥10 years old when last recaptured. If a negative effect on survival is manifest in the days immediately after blood sampling of an individual, it could potentially be determined by estimating daily survival of birds after sampling. However, within-season survival must be estimated for each colony site separately, because each is sampled on different days (Brown and Brown 2004), and we did not have enough data (i.e., birds bled) when divided by colony site to attempt this sort of finer-grain analysis.

As in any study of survival in an open population, we could estimate only local or apparent survival; birds permanently emigrating from the study area between years cannot be separated from those that died. For example, it is possible that bled birds dispersed farther between years or were more likely to permanently emigrate than non-bled birds, resulting in the higher apparent survival probabilities for Cliff Swallows that were not blood-sampled. We have no way to estimate permanent emigration, because band recoveries of Cliff Swallows outside the study area are few. However, if this occurred, it suggests that bleeding can affect movement behavior in profound ways.

Our models revealed an effect of colony fumigation status on the probabilities of annual survival and recapture. This is most likely because birds at fumigated (parasite-free) sites have higher overall annual (and daily) apparent survival in our study area (Brown and Brown 1996, 2004; Brown et al. 2008; Table 3). Birds bled at non-fumigated sites had a greater percent reduction in survival than birds at fumigated sites, and this result held for birds from which both small and large amounts of blood were taken.

We do not know precisely how blood sampling led to a reduction in survival of Cliff Swallows. Among captive birds of different species, blood loss results in drops in blood pressure, increased release of circulating catecholamines, aldosterone, and arginine vasotocin, decreased cardiac output, increased heart rate, and decreases in hematocrit, hemoglobin, and plasma proteins (Gildersleeve et al. 1985, Radke et al. 1985, Sturkie 1986). Blood volume is restored initially and relatively quickly (at least in captive birds) by absorption of tissue fluid, but hemoglobin and hematocrit concentrations can remain low for variable lengths of time and may result in anemia (Ploucha et al. 1981, Fair et al. 2007). Survival could be negatively affected by anemia, dehydration, reduced oxygen metabolism, or hematomas in the wing caused by blood sampling, especially in highly aerial birds such as Cliff Swallows that spend considerable time each day in flight. Reduction in hemoglobin concentration seems to be a particularly serious consequence of blood loss and may lead to increased respiration rates and greater energy expenditure (O'Brien et al. 2001, Carleton 2008).

The physiological effects of hemodilution (e.g., anemia) may be especially severe in individuals that are already stressed by other environmental factors (Fair et al. 2007). The greater reduction in survival for birds bled at non-fumigated colonies than at parasite-free sites may reflect the greater stress levels of Cliff Swallows experiencing ectoparasitism (Raouf et al. 2006) and, thus, their inability to deal with the additional stress of blood sampling. Some evidence indicates that birds under pressure from hematophagous ectoparasites have lower hematocrit (reviewed in Fair et al. 2007) and reduced hemoglobin (O'Brien et al. 2001, Carleton 2008) and, thus, the additive effect of blood sampling may have depressed hematocrit or hemoglobin, or both, of birds from non-fumigated sites to deleteriously low levels. In the absence of ectoparasites such as Swallow Bugs, Cliff Swallows may be better able to endure various investigator-induced stresses, although blood sampling seriously affected survival even at fumigated sites.

Cliff Swallows (and other birds) may vary in their sensitivity to the effects of blood collection at different times in the nesting cycle. For example, early in the season, when these birds can be food-stressed by periodic bouts of cold weather (Brown and Brown 1996, 1998, 2000) and must forage for long periods, the associated effects of hemodilution may be worse. By contrast, late in the summer or during periods of incubation before their body mass drops to the lower levels characteristic of the nestling-rearing period (Brown and Brown 1996), Cliff Swallows may be better able to compensate for the energetic consequences of blood loss. Our study was not designed to address these possibilities, and to do so would likely require blood sampling at different times during the summer and measurement of within-season survival (*sensu* Brown and Brown 2004) after blood collection.

Perhaps Cliff Swallows, relying so much on flight, are unusually susceptible to the negative effects of blood sampling. However, given that we found that survival was affected even when small amounts of blood representing only 0.3–0.6% of body mass were taken, the commonly used guidelines specifying an amount of blood equal to 1% of body weight for any one sampling event or 2% over a two-week period (Gaunt and Oring 1999) may be inappropriate for small birds such as swallows. Even for Cliff Swallows designated as having been bled a "large amount" (0.9–1.2% of body mass), in practice we sometimes took less than this from this group of birds because one or more tubes were not full. With the 1% rule, workers may be collecting too much blood if they hope to avoid effects on survival. Our results suggest that when even larger amounts of blood (≤5% of body weight) are collected (Wingfield and Farner 1976, Stangel 1986), survival should be carefully evaluated using controlled comparisons with non-bled individuals. Studies involving repeated blood sampling over short periods, such as those quantifying the stress response in birds in which blood is taken at intervals to measure hormone levels (e.g., Wingfield et al. 1992, Silverin 1998, Dufty 2008), should be especially sensitive to their potential effects on subsequent survival.

Depending on their skill in taking blood samples, different workers may cause different levels of stress to birds and, thus, different effects on survival. Four trained investigators bled birds in our study. Our analyses were not designed to tease apart worker effects, which would have been difficult because different workers generally bled birds in different years (Table 1) and, thus, potential effects of different workers would be confounded with the yearly effects on survival that are pronounced in Cliff Swallows at our study site (Brown and Brown 1996). However, we found the same general patterns in all years, which suggests that our results were not solely artifacts of varying skill levels of the people taking the blood.

Method of bleeding may also affect the extent to which survival is potentially affected by blood sampling. All our samples were taken with brachial venipuncture, which seems to be most common among ornithologists. However, some avian biologists and virologists use jugular blood sampling (Franks 1967, Utter et al. 1971, Hoysak and Weatherhead 1991, Lanctot 1994, Komar et al. 2003, Garvin et al. 2004, Perkins et al. 2004). More rarely, samples are taken by heart puncture or from the tibiotarsus (Gaunt and Oring 1999). Further studies similar to the present one are needed for each of the different collection methods, because each may cause different kinds or levels of stress in birds.

Our results suggest caution in collecting blood from wild birds and reveal the need for additional work, on more species, that formally estimates subsequent survival of bled and non-bled birds captured simultaneously. This is especially the case for threatened or endangered species, where blood sampling and other experimental manipulations should be evaluated thoroughly for their potential effects on survival and population size (Ardern et al. 1994, Peery et al. 2006). Scientists always have the ethical responsibility to use invasive techniques such as blood sampling as infrequently as possible. Our results emphasize the importance of considering alternatives to blood sampling, such as assaying glucocorticoid hormones from feces (e.g., Washburn et al. 2003), collecting DNA samples with oral swabs or from feathers, eggshells, embryos, or skin (e.g., Marsden and May 1984, Taberlet and Bouvet 1991, Groombridge et al. 2000, Strausberger and Ashley 2001, Handel et al. 2006, Harvey et al. 2006, Lecomte et al. 2006), and surveying for viruses using oral or cloacal swabs (e.g., Komar et al. 2003, Padgett et al. 2006). Because studies using blood sampling typically involve relatively small numbers of individuals, past attempts to test whether blood collection impairs survival have often had low statistical power to detect effects, meaning that differences are rarely found. This perhaps has contributed to the conventional wisdom that blood sampling is generally benign. Our results in Cliff Swallows underscore the importance of having large enough sample sizes of bled and non-bled birds to yield high power for detecting effects if they exist and the need to measure actual survival (rather than only recapture percentage) in studying the effects of blood sampling in birds.

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